Shoichi KAWANO* & Masaaki IHARA**: **Chromosome morphology of *Caulophyllum robustum* (Podophyllaceae) and its systematic implications**

河野昭一*・井原正昭**：ルイヨウボタンの核型と二三の進化学上の問題について

Caulophyllum is a small genus of the Podophyllaceae (cf. Hutchinson 1959), comprising only two species: *C. robustum* Maxim. of eastern Asia and *C. thalictroides* (L.) Michx. of eastern North America. These two species are, however, often considered to be conspecific, e. g., Kitamura (in Kitamura and Murata 1962) regards these plants as two geographical subspecies of the single species, i. e., *C. thalictroides* ssp. *thalictroides* and ssp. *robustum* (Maxim.) Kitam.

The North American species, *C. thalictroides*, was first cytologically studied by Langlet (1928), who exhibited the somatic chromosome number of this plant to be $2n=16$; whereas the gametic number $n=8$ was reported by Matsuura and Suto (1935) for the Asiatic species. A more detailed karyological observation was recently made by Moore (1963) for North American *C. thalictroides* var. *thalictroides* and var. *giganteum*. According to him, both varieties are diploid with $2n=16$ chromosomes and have exactly the same karyotype, i. e., the complement consists of five pairs of chromosomes with a subterminal constriction, two pairs, one large and one small, of metacentric chromosomes, and one contrastingly small pair that has a subterminal constriction (cf. Fig. 3).

Since the exact chromosome morphology of the Asiatic species, *C. robustum*, remained so far unknown, a critical karyological analysis was made in the present study for *C. robustum* to compare with the karyotype of North American *C. thalictroides*. Also, several problems relating to their systematic status are briefly discussed.

Material and Methods

Three clones of *C. robustum* were collected at the margin of the oak-maple forests by Ryudzu-no-taki, Nikko, Tochigi Pref., Japan, in summer, 1965, and since then were cultivated in clay pots. The preparation was made by using a modification of oxyquinoline acetic orcein squash method (cf. Kawano 1965). Voucher specimens are preserved in TI.

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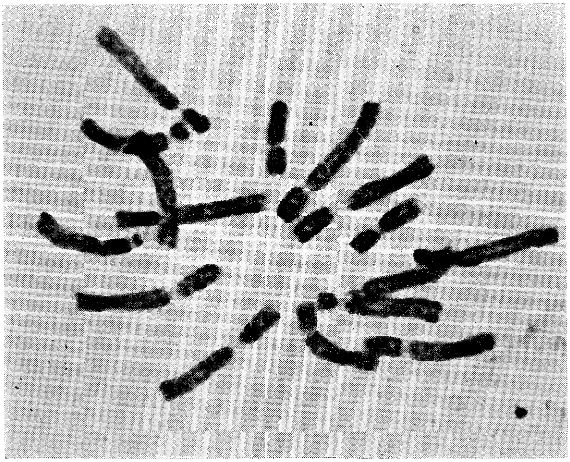

Fig. 1. Somatic chromosomes of *Caulophyllum robustum*, 2n=16.

Results and Discussion

The present analysis demonstrates that the materials examined are also diploid with 2n=16 chromosomes, the results corroborating the previous observation made by Matsuura and Suto (l. c.). A closer examination of the karyotype reveals that the chromosome complement consists of three pairs with a submedian constriction (Figs. 1 and 2; Tab. 1, No. 1, 2 and 3), three pairs with somewhat a subterminal constriction (No. 4, 5 and 6), one pair of satellite chromosomes with nearly a terminal constriction, and one contrastingly small pair with a submedian constriction (No. 8). Therefore, the karyotype formula for this species may roughly be expressed as follows: $K(2n)=16=6J_1+6J_2+2J_1^{cs}+2j$.

As can be readily seen from the karyograms prepared for both *C. thalictroides* and *C. robustum* (cf. Figs. 2 and 3), these two species show remarkably different karyotypes, despite the fact that they show very slight phenotypic differences in gross morphology (cf. Fig. 4). A very sharp morphological distinction detected between them is only in leaves (though even this occasionally obscured by the

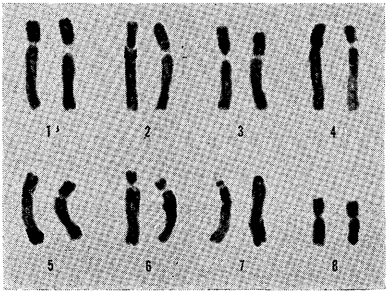

Fig. 2. Somatic chromosomes of *C. robustum*, 2n=16. Karyogram produced from Fig. 1.

Tab. 1. Somatic chromosomes of *Caulophyllum robustum* Maxim. (cf. Fig. 2)

Chromosomes	Length of arms in μ	Total length in μ	Index
1.	2.7+7.8	10.5	0.35
	3.3+7.5	10.8	0.45
2.	3.3+7.5	10.8	0.45
	3.3+7.2	10.5	0.46
3.	3.3+6.3	9.6	0.52
	3.0+6.3	9.3	0.48
4.	2.7+8.1	10.8	0.33
	2.4+8.1	10.5	0.30
5.	2.1+6.6	8.7	0.32
	2.1+6.3	8.4	0.33
6.	1.8+7.2	9.0	0.25
	1.5+6.9	8.4	0.22
7.	0.6+7.2	7.8	0.08
	0.6+7.5	8.1	0.08
8.	2.1+3.6	5.7	0.58
	2.1+3.3	5.4	0.64

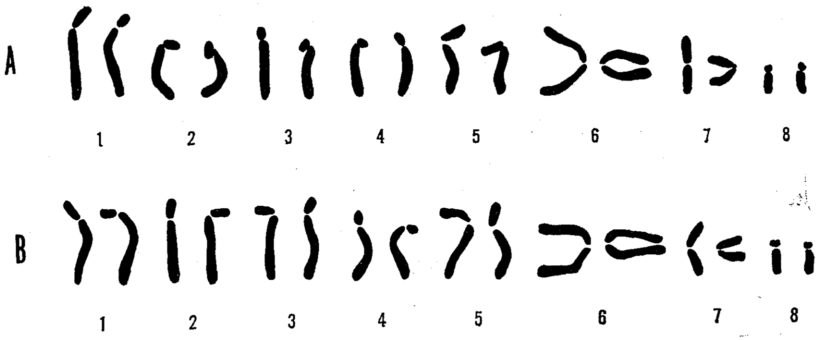

Fig. 3. Somatic chromosomes of *C. thalictroides* var. *thalictroides* (A. 2n=16) and var. *giganteum* (B. 2n=16). Karyograms produced from drawings presented by Moore (1963).

occurrence of interconnecting forms—cf. Fig. 4-B), i.e., in *C. robustum* terminal leaflets are obovate-cuneate with rather deep, sharply pointed lobes but lateral

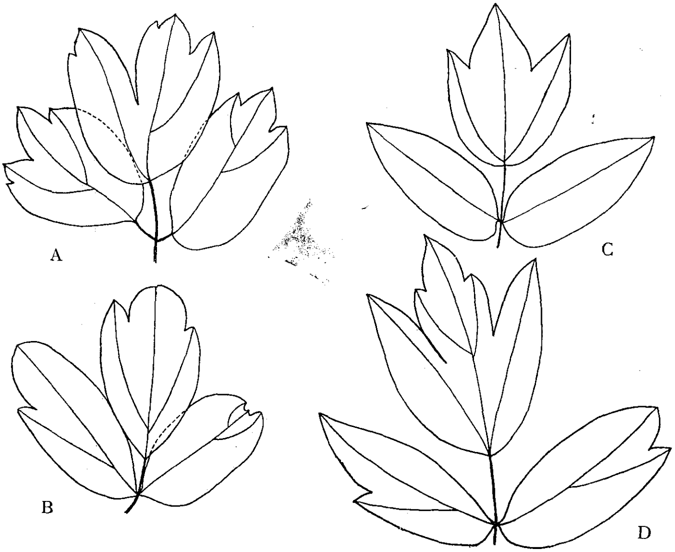

Fig. 4. Illustrating leaflets of the large triternately compound leaf of *Caulophyllum*: A. *C. thalictroides* from Oka, Quebec, Canada (collected by S. Kawano in 1963): B. *C. robustum* from Irikawa, Isl. Sado, Japan; C. from Mt. Ontake, Kiso Honshu, Japan; D. from Kitaura, Oga Peninsula, Akita, Honshu, Japan.

leaflets oblong-ovate, acute at apex and always sessile (cf. Fig. 4-C and D); whereas *C. thalictroides* has terminal and lateral leaflets that are usually obovate-cuneate, 2-3-lobed, lateral leaflets usually being shortly petiolate (Fig. 4-A). According to Moore (l. c.), North American *C. thalictroides* (including var. *giganteum*) carries at least two pairs, one large and one small, of characteristic metacentric chromosomes among the eight pairs of somatic chromosomes (Fig. 3, No. 6 and 7); whilst *C. robustum* possesses no such metacentric pairs but one pair of distinctive satellite chromosomes with a terminal constriction (Fig. 2, No. 7). Some of the remaining chromosomal pairs in the complements of both species may represent homologous chromosome sets. The origin of such a karyological differentiation as shown above is, however, not explicable in terms of simple structural changes occurred in some chromosomal pairs of both species.

On the basis of his cytological observations, Moore (l. c.) postulated a rather simple process of karyological evolution from the ancestor of *Caulophyllum* that possibly had $2n=12$ chromosomes: first, one chromosome of the hypothetical ancestral pair formed complementary telocentrics which in turn became the two isochromosomes (cf. Fig. 3, No. 6, 7); then at meiosis these would form a trivalent with the remaining normal chromosome and the resulting gametes would receive either the normal original karyome or the original karyome plus the two isochromosomes and less the chromosome from which the latter type of gametes would be formed a plant with two of each of the new isochromes, and thus a somatic number higher by two than that of the ancestral plant. He further advanced a presumption that the smallest chromosome pair (Fig. 3, No. 8) was formed by subsequent aberrations, i. e., by the disjunction of a bivalent of chromosome No. 7 which differed by an inversion in one arm and therefore produced a chromatid bridge and fragments; the ruptured bridge would then constitute the short arm of one chromatid of each disjunct chromosome. As a result, two types of gametes would be formed, those with a normal chromosome No. 7 and those with a chromosome No. 7 lacking most of one arm. Possibly gametes containing both types were also formed and only zygote with a pair of each type of chromosome were viable, others lacking genic balance. Such a zygote would contain unaltered ancestral chromosomes, one pair of long isochromosomes, one pair of short isochromosomes and one pair of short isochromosomes lacking most of one arm—karyome now as seen in *C.thalictroides*. Accordingly, the complement contains three new pairs of chromosome (No. 6, 7, 8) derived from one pair which is no longer present.

Moore considered here that the basic karyotype of contemporary *Caulophyllum* is as such found in *C. thalictroides*. However, our present finding, i. e., *C. robustum* which is regarded to be very closely related to North American *C. thalictroides*, possesses no such metacentric chromosomal pairs and rather, a markedly distinct karyome suggests that there may have been some other entirely different, complicated processes of structural modifications in the karyological evolution and speciation of *Caulophyllum* species. With our very limited present-day knowledge, it is difficult to interprete the origin of $2n=16$ (the basic number of $x=8$) found in *Caulophyllum* in terms of only a simple numerical and net increase of the chromosomes from the ancestral plants with $2n=12$ ($x=6$) chromosomes. It is certainly known that genera such as *Achlys*, *Bongardia*, *Diphylleia*, *Epimedium*, *Jeffersonia*, *Podophyllum*, all referred to the Podophyllaceae (cf. Hutchinson l. c.) and some of them indeed be related to *Caulophyllum*, have $2n=12$ chromosomes (Langlet l. c.; Miyaji 1930; Toren 1950). Another genus, *Ranzania*, which is also referred to this group, is known to possess $2n=14$ chromosomes, however (Miyaji l. c.). We could easily see, judging from their enormous diversities found in gross morphology, that those genera cited above are very heterogeneous, each genus being very specialized (Note, for example, the extremely specialized flowers of *Epimedium*, etc.), suggesting their prominently ancient origin and differentiation, although most of them are nowadays associated with mesothermic moist temperate deciduous (or occasionally boreal) forests of Arcto-Tertiary origin. The contemporary geographical areas of *Caulophyllum* suggest that this genus also has maintained its historical-ecological connection with this mesothermic temperate vegetation like other so-called Arcto-Tertiary elements (Fig. 5, map; cf. Li 1952; Koyama & Kawano 1964; Kawano & Iltis 1966). As to the true evolutionary relationships of *Caulophyllum* with other genera belonging to the Podophyllaceae and the taxonomic status of both *C. robustum* and *C. thalictroides*, however, further critical biosystematic studies will be needed.

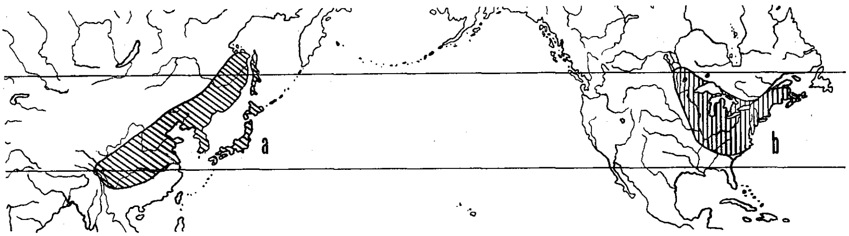

Fig. 5. The geographical areas of *Caulophyllum*. a: *C. robustum*; b: *C. thalictroides*.

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中国雲南省揚子江上流地域より北太平洋沿岸沿いの温帯―冷温帯林下にやや広く分布するルイヨウボタン (*Caulophyllum robustum*) は北米東部の温帯性落葉広葉樹林下に生育する *C. thalictroides* と非常に近縁な植物として知られている。この両種は共に2倍体 (2n=16) であることがわかっている。最近 Moore (1963) は北米の *C. thalictroides* とその変種 var. *giganteum* でくわしく核型を報告し，ルイヨウボタン属の進化学的位置を論じた。一方，アジアのルイヨウボタンの正確な核型は不明のままであったので，著者らはまずそれを明らかにし，さらに二三の系統学上の問題を論議した。

Moore は *C. thalictroides* で8対の体細胞染色体組のうちに，長短2対の特徴的な中部に狭窄を持つ V および v 型染色体のあることを報じ，これらはもはや現存しない次中部に狭窄をもつ J 型の1対から構造変化で作られた腕相同染色体であろうと推論した。さらに次端部に狭窄をもつ最も短い j 型の1対はさらに腕相同のv型から腕の一部を失って生じたものであるとした。

一方著者らは邦産のルイヨウボタンで観察を行なった結果，この植物では8対の染色体組の内には中部に狭窄をもつ V, v 型染色体対は1対もなく，1対の特徴的な端部に狭窄をもつ仁染色体と1対の短い次中部に狭窄をもつ染色体，次中部もしくは次端部にそれぞれ狭窄をもつ6対などよりなり，基本的構成上で *C. thalictroides* とは異なることが明らかになった。これらの8対の染色体組のうちの何対が互いに相同であるかは現在では判じようがない。少なくとも Moore が推論した 2n=12 をもつ祖型植物よりの構造変化による染色体増加だけでルイヨウボタン属の核型進化の過程を論じさるのはあまりに不充分であり，*Caulophyllum* とミヤオソウ科 (Podophyllaceae) に属する *Diphylleia*, *Podophyllum*, *Jeffersonia*, *Ranzania* など他の属とのよりはっきりした類縁関係の解明は将来の研究に待つところが多い。

新刊紹介

□カラー山の花 I, II. (1967) 東京山と渓谷社各々 pp. 200 ¥480 昨年出て好評だったIに加えて，Iに登載もれのものを集めてIIと共に揃えて出版された。必らずしも表題のように高山や深山の花とは限らぬが，2頁おきの見開き写真に 2—3 種を載せるからちょっとした図鑑である。写真が美しく詳明で，多くのアップ写真は見逃がし勝ちな花の細部や立体的な構造を再認できる点でよい。色は美しすぎる位である。

（前川文夫）